

COMPOSITION, STRUCTURE, AND DYNAMICS OF VEGETATION IN FIFTEEN BEAVER-IMPACTED WETLANDS IN WESTERN MASSACHUSETTS

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ABSTRACT. Quantitative investigations of vegetational composition and structure in 15 beaver-impacted wetlands in Franklin and Hampshire Counties, Massachusetts, were conducted between 1980 and 1995. Four wetland types were identified based on species composition. Five distinctive physiographic zones, each with a characteristic assemblage of plant species, and three successional pathways were observed in the study sites. While soil moisture is clearly a strong influence on plant community structure and composition in beaver-impacted wetlands, hydrological dynamics including frequency, duration, and extent of flooding appear more influential than depth to water table.

Key Words: Beaver (*Castor canadensis*), hydrology, wetland succession, Massachusetts

In the seventy-five years since its return to Massachusetts, the beaver (*Castor canadensis*) has reestablished itself as an important member of the state's fauna and as a powerful force in shaping the region's landscape. In some areas of western Massachusetts nearly every small stream is inhabited, and beavers are increasingly colonizing larger streams as well as rivers, ponds, and lakes.

Foraging activities of the beaver remove large amounts of woody vegetation and thus influence forest composition and structure (Hall 1960; Rutherford 1955). Dam construction alters many aspects of hydrology in the riparian zone including stream velocity, sediment transport, and soil and water chemistry (Naiman et al. 1988; Smith et al. 1991).

Occupation of a site by beavers may continue for a number of years, but eventually a colony will either migrate to another site as food supply dwindles or will be removed by trapping, natural predation, or disease. Even as an unmaintained beaver dam deteriorates, it continues to impound water, especially following spring meltout or heavy precipitation events during the growing

season. Many abandoned beaver dams thus influence stream hydrology for years, even decades, following abandonment. Old dams, lodges, food caches, and channels provide topographic complexity which, when combined with temporal fluctuations in water level, contribute to a particularly rich vascular flora in abandoned beaver wetlands in terms of both species richness and the presence of uncommon and rare species (McMaster and McMaster 2000).

Plant succession in freshwater wetlands has long been a subject of interest to ecologists. Weaver and Clements (1938), Oosting (1956), and others describe a predictable sequence of vegetation types from aquatics to emergents to shrubs and trees, ultimately leading to a relatively stable terrestrial community. The presence of many forested wetlands in the glaciated northeastern United States, particularly those dominated by *Acer rubrum* L. and/or a few other tree species capable of tolerating saturated soils (Golet et al. 1993), suggests that wetland succession in the region is more complex than previously thought, and may be influenced by topographic and geologic factors. Beaver activity may be yet another factor influencing both short-term and long-term wetland succession in the region.

This study was begun by Nancy D. (Mosher) McMaster in 1980. She initially sampled all sites from 1980–1984 and began resampling in 1985 (McMaster 1989). Upon her death in 1990, Robert T. McMaster resumed the sampling schedule, employing the transects and methodology of the previous work. This paper presents classifications of the 15 western Massachusetts study sites and the plant communities they support, a model of plant succession, and an analysis of factors influencing vegetation structure and dynamics in beaver-impacted wetlands.

MATERIALS AND METHODS

Study sites. The 15 study sites are located on first and second-order streams on the eastern slope of the Berkshire Plateau in Franklin and Hampshire Counties, Massachusetts (Table 1). Sites range in area from 0.6 to 8.0 ha and in elevation from 164 to 465 m above sea level.

Previous to the reintroduction of beavers in western Massachusetts in the 1920s, all study sites were upland bordering a narrow stream course. Two sites are referred to as “pasture” in

Table 1. County, watershed, elevation above sea level, area, and age since last beaver occupation (as of 1995) for the 15 study sites. ¹Refers to the Mill River with headwaters in Conway and which enters the Connecticut River at Hatfield. ²Refers to the Mill River with headwaters in Goshen and Ashfield and which enters the Connecticut River at Easthampton. Reprinted from McMaster and McMaster (2000).

Site	County	Watershed	Eleva- tion (m)	Area (ha)	Age (years)
Ashfield 1	Franklin	Westfield River	417	3.8	20
Ashfield 2	Franklin	Westfield River	417	1.4	40
Ashfield 3	Franklin	Westfield River	393	2.5	1
Ashfield 4	Franklin	Mill River ¹	453	6.2	1
Ashfield 5	Franklin	Mill River ¹	453	2.5	1
Ashfield 6	Franklin	Deerfield River	465	1.8	16
Conway 1	Franklin	Mill River ¹	369	1.8	25
Conway 2	Franklin	Mill River ¹	362	2.5	35
Conway 3	Franklin	Mill River ¹	338	3.2	18
Conway 4	Franklin	Mill River ¹	329	1.0	15
Conway 5	Franklin	Mill River ¹	243	3.5	16
Goshen 1	Hampshire	Mill River ²	417	2.1	18
Williamsburg 1	Hampshire	Mill River ¹	220	7.8	26
Williamsburg 2	Hampshire	Mill River ²	164	0.6	16
Worthington 1	Hampshire	Westfield River	375	8.0	10

old deeds; a narrow cart road dating to at least the mid-nineteenth century crosses one site; stone walls dissect four sites; submerged stumps and standing dead trees, mostly of *Pinus strobus* L., *Tsuga canadensis* Carrière, *Picea rubens* Sarg., and *P. abies* (L.) Karst, are present in eight sites (McMaster 1989). All sites have a history of beaver occupation but were unoccupied when first sampled. Details of site selection may be found in McMaster and McMaster (2000); vegetation maps of each site may be found in McMaster (1997).

Site histories were reconstructed by examination of U.S.D.A. Soil Conservation Service maps and panchromatic black and white aerial photographs (scale 1:24,000), U.S. Geological Survey maps, deeds, town histories, by communication with property owners, and by field observation. Sites were monitored regularly for presence or absence of active beaver colonies throughout the period of the study. Site age (i.e., number of years since last beaver occupation; when a site is reoccupied, its age becomes

zero) was determined from communication with property owners or local residents and from direct observation.

Vegetation sampling. Transects were established across each site parallel to the abandoned beaver dam. Each transect was placed within a zone of relatively homogeneous vegetation based upon life form of the dominant vegetation. Transects extended across the wetland to the upland margin on each side of a site. Number of transects per site ranged from 3 to 9 depending on the size and complexity of the site.

Along each transect, 0.5 m $\times$ 0.5 m quadrats were located at 2 m intervals. Number of quadrats per transect ranged from 6 to 74 (mean = 24.4). Within each quadrat, percent cover was determined by visual estimate for all vascular plants and for those nonvascular plants with cover $> 1\%$.

All sites were originally sampled in midsummer between 1980 and 1984 (McMaster 1989; Mosher 1981). Three sites (Conway 1, 2, and 3) were resampled at five-year intervals. The remaining 12 sites were to be resampled at ten-year intervals when possible. Seven of these were resampled on schedule. Ashfield 3, which had been reoccupied by beavers in 1992, was resampled in 1993 after the site was once again abandoned. Four sites originally sampled in 1984 (Ashfield 6, Conway 5, Goshen 1, and Worthington 1) were not resampled in 1994 or subsequently due to continued beaver occupation which made sampling impractical. All sites were revisited at regular intervals and beaver activity recorded.

Nomenclature for vascular taxa follows Gleason and Cronquist (1991). A complete list of the vascular flora of the 15 sites appears in McMaster and McMaster (2000).

Collection of hydrologic and sediment data. Observation wells of perforated, 1 $\frac{3}{4}$ -inch diameter PVC pipe, 1 m in length, were placed near the midpoint of 33 transects in 10 unoccupied sites, and ground water levels were monitored biweekly from late spring to late fall, 1995. For sites with standing water, staff gauges were monitored biweekly during the summers of 1994 and 1995.

Field analysis of water samples was accomplished in June, 1995, using an Accumet 1002 Field pH Meter for pH [referred to below as pH (field)], a YSI Model 34 Conductance-Resistance

Meter for specific conductance, and a YSI Model 58 Dissolved Oxygen Meter for dissolved oxygen concentration. One 100 ml water sample was collected immediately above the dam at each site in September, 1995, transported to the laboratory, and stored in the dark at 4°C. The Accumet 1002 Field pH Meter was also used to measure pH for these samples, referred to below as pH (lab). Alkalinity of one to three samples from each site was determined by titration with 0.01 M HCl according to the protocol in American Public Health Association (1989).

Depth of organic material was measured using a 2 m graduated steel rod. Number of measurements per transect ranged from 2 to 13 (mean = 6). Depths greater than 2 m were recorded as 2 m and calculations based upon those estimates are noted below.

Data analysis. A modification of the importance value of Mueller-Dombois and Ellenberg (1974) was calculated by summing relative percent cover and relative frequency for each species in all quadrats of a transect and is referred to below as MIV. Sites and transects were ordinated using two-way indicator species analysis (TWINSPAN; Hill 1979). Only species with $MIV \geq 5$ were used in this analysis. Default values were used for all parameters except cut values which were set at 5, 10, 20, and 30. Data were then ordinated with detrended correspondence analysis using the software program CANOCO (ter Braak 1988) including only species with $MIV \geq 5$ in each transect and setting all parameters at default values. Transects identified as outliers were removed and the analysis repeated to permit a more precise ordination of the remaining data as recommended by Gauch (1982).

When a transect was sampled more than once, each resampling was treated as a separate transect for all ordinations. This approach has the advantage of revealing temporal changes in composition. In analyzing the resulting ordination data, however, it must be remembered that resampled transects have greater influence on the ordination than those sampled only once. Similarity coefficients used to compare species composition of sites included those of Jaccard, Ellenberg, Sørensen, Gleason, and Spatz as described in Mueller-Dombois and Ellenberg (1974).

Possible relationships between abiotic parameters and the species composition of vegetation were examined using TWINSPAN and canonical correspondence analysis using the CANOCO software program (ter Braak 1988). Because collection of abiotic data

was completed during the summer of 1995, only vegetation data for the 48 transects in 11 sites sampled during the period 1992–1995 were used for this analysis. Canonical correspondence analysis was employed to examine relationships between species composition and pH, conductivity, alkalinity, dissolved oxygen concentration, depth of organic matter, distance to water table, and site age. Default values were used for all parameters in this analysis. Where data were absent, means for that transect were substituted as recommended in ter Braak (1988).

RESULTS

Site classification. Based on data from the most recent sampling, the 15 study sites were clustered into four groups (I–IV) with TWINSpan. Data for each site and each TWINSpan group are presented in Tables 2 and 3.

Group I included three sites dominated by the shrubs *Alnus incana* and *Spiraea alba* var. *latifolia*. Site age ranged from 16 to 26 years. These sites were characterized by relatively low water table, very low percent cover of *Sphagnum* spp., and high percent cover of trees and shrubs. Cover of tussock-colonizing graminoids was variable, ranging from 1.5 to 54.6%. Depth of organic matter ranged from 65.6 to 113.1 cm (Table 2). This group corresponds to “shrub swamp” as defined by Reschke (1990).

Group II included five sites dominated by tussock-colonizing graminoids *Calamagrostis canadensis* and *Carex stricta* and/or mud flat colonizers *Leersia oryzoides* and *Eleocharis* spp. Site age ranged from 1 to 40 years. Like Group I, these sites were characterized by relatively low water table and low percent cover of *Sphagnum* spp., but with a low percent cover of trees and shrubs, as well. Cover of tussock-colonizing graminoids ranged from 0 to 56.5%. Depth of organic matter ranged from 65.7 to 154.3 cm (Table 2). This group corresponds to “shallow emergent marsh” as defined by Reschke (1990).

Group III included three sites dominated by *Calamagrostis canadensis* or *Typha latifolia* with large areas of standing water usually covered with *Najas flexilis* or *Lemna minor*. Two of the three sites had been abandoned only one year when sampled; one site had been abandoned 16 years. These sites were characterized by high water table, low percent cover of *Sphagnum* spp., and low percent cover of trees and shrubs. Cover of tussock-coloniz-

Table 2. Site age, % cover of trees and shrubs, % cover of tussock-colonizing graminoids, % cover of *Sphagnum* spp., mean depth to water table, and mean depth of organic matter for 15 study sites and four TWINSPAN groups. – Indicates data not available. *Indicates sites with measurements of organic matter > 200 cm (see Materials and Methods). “FL” indicates sites that were flooded in 1995 when water table data were collected. Site abbreviations: Ashfd. = Ashfield; Willb. = Williamsburg; Worth. = Worthington.

Site	Site Age (years ± sem)	% Cover of Trees and Shrubs	% Cover of Tus- sock- Co- lon- izing Gram- inoids	% Cover of <i>Sphag- num</i> spp.	Mean Depth to Water Table (cm ± sem)	Mean Depth of Organic Matter (cm ± sem)
Group I						
Willb. 1	26	52.2	54.6	2.7	13.9 ± 2.2	113.1 ± 9.1*
Willb. 2	16	70.9	8.2	2.7	31.4 ± 3.3	113.1 ± 11.9*
Conway 3	18	38.2	1.5	0.1	7.5 ± 1.4	65.6 ± 5.9
MEAN	20.0 ± 3.1	53.8	21.5	1.8	15.0 ± 1.7	95.4 ± 5.7
Group II						
Ashfd. 6	16	17.4	7.2	0.0	FL	–
Worth. 1	10	14.3	0.0	2.5	FL	–
Ashfd. 1	20	9.9	56.5	2.1	16.1 ± 2.2	154.3 ± 12.8*
Ashfd. 2	40	11.8	47.0	12.0	2.1 ± 0.7	136.5 ± 15.2*
Ashfd. 3	1	1.9	25.9	0.2	14.2 ± 1.7	65.7 ± 4.5
MEAN	17.4 ± 6.5	11.1	27.3	3.4	12.0 ± 1.3	106.7 ± 7.0
Group III						
Ashfd. 4	1	8.7	0.3	0.0	5.6 ± 1.5	89.0 ± 9.4*
Ashfd. 5	1	11.1	35.7	0.3	FL	54.1 ± 5.2
Conway 5	16	30.5	13.9	0.0	FL	–
MEAN	6.0 ± 5.0	16.7	16.6	0.1	5.6 ± 1.5	81.9 ± 7.8
Group IV						
Goshen 1	18	40.1	5.2	1.3	–	–
Conway 4	15	30.1	5.5	15.7	6.1 ± 1.1	46.5 ± 5.0
Conway 1	25	8.3	2.0	26.9	2.4 ± 1.2	84.5 ± 8.3
Conway 2	35	41.0	0.5	35.6	1.8 ± 0.7	189.1 ± 10.9*
MEAN	23.3 ± 8.9	29.9	3.3	19.9	3.4 ± 0.6	94.6 ± 8.9

Table 3. Water chemistry characteristics for 15 study sites and four TWINSPAN groups. Group means include only 11 sites (*) resampled from 1992–1995. – Indicates data not available. See Table 2 for site abbreviations.

Site	pH Lab (± sem)	pH Field (± sem)	Alkalinity (mg/l ± sem)	Conductivity (mhos ± sem)	Dissolved Oxygen Concentration (mg/l ± sem)
Group I					
*Willb. 1	6.10	6.16 ± 0.03	13.0 ± 2.5	63.8 ± 2.4	5.4 ± 1.0
*Willb. 2	6.95	6.36 ± 0.08	27.4 ± 1.8	60.0 ± 0.0	9.5 ± 0.3
*Conway 3	6.61	6.40 ± 0.05	21.5 ± 7.5	81.3 ± 1.3	–
MEAN	6.55 ± 0.25	6.34 ± 0.05	20.6 ± 3.4	67.0 ± 2.7	8.0 ± 0.8
Group II					
Ashfd. 6	7.04	6.19 ± 0.20	26.0 ± 7.4	108.3 ± 4.0	3.8 ± 0.6
Worth. 1	5.22	4.84 ± 0.05	2.0 ± 1.5	42.5 ± 7.5	–
*Ashfd. 1	6.96	6.42 ± 0.14	28.1 ± 2.8	166.7 ± 1.7	7.2 ± 0.2
*Ashfd. 2	6.45	6.55 ± 0.00	19.8 ± 4.3	158.3 ± 1.7	7.1 ± 0.3
*Ashfd. 3	5.94	5.76 ± 0.11	1.3 ± 0.3	35.7 ± 0.3	12.7 ± 1.1
MEAN	6.45 ± 0.29	6.28 ± 0.11	18.1 ± 4.8	116.5 ± 17.6	9.1 ± 0.9
Group III					
*Ashfd. 4	6.74	6.40 ± 0.18	33.8 ± 16.8	118.0 ± 13.6	5.6 ± 0.7
*Ashfd. 5	6.16	6.26 ± 0.29	21.0 ± 1.0	150.0 ± 10.0	2.2 ± 1.2
Conway 5	6.53	6.45 ± 0.12	29.3 ± 9.8	111.7 ± 9.3	1.8 ± 0.2
MEAN	6.45 ± 0.29	6.34 ± 0.11	26.1 ± 6.2	116.7 ± 11.1	4.0 ± 0.7
Group IV					
Goshen 1	6.70	6.82 ± 0.30	19.8 ± 1.3	168.0 ± 3.4	3.2 ± 0.5
*Conway 4	6.53	5.22 ± 0.05	17.8 ± 1.3	57.0 ± 1.2	–
*Conway 1	6.40	6.39 ± 0.04	14.5	143.8 ± 2.4	–
*Conway 2	5.64	5.27 ± 0.07	2.8 ± 1.3	45.8 ± 4.0	–
MEAN	6.19 ± 0.28	5.75 ± 0.17	11.1 ± 3.5	79.7 ± 9.6	–

Table 4. Modified importance values (MIV) of *Sphagnum* spp., *Calamagrostis canadensis*, and *Carex stricta* in 11 sites. Sites are arranged in order of increasing pH (lab).

	Site pH (lab)	<i>Sphagnum</i> spp.	<i>Calamagrostis</i> <i>canadensis</i>	<i>Carex</i> <i>stricta</i>
Conway 2	5.64	43.4	0.0	1.3
Ashfield 3	5.94	0.6	27.7	13.0
Williamsburg 1	6.10	5.7	35.3	51.9
Ashfield 5	6.16	0.8	66.8	6.9
Conway 1	6.40	30.9	0.0	2.6
Ashfield 2	6.45	21.1	23.2	71.8
Conway 4	6.53	15.8	0.0	9.2
Conway 3	6.61	0.3	0.0	3.3
Ashfield 4	6.74	0.0	0.0	1.5
Williamsburg 2	6.95	3.2	1.8	8.3
Ashfield 1	6.96	4.2	57.6	53.3

ing graminoids ranged from 0.3 to 35.7%. Depth of organic matter ranged from 54.1 to 89.0 cm (Table 2). This group corresponds to “shallow emergent marsh” as defined by Reschke (1990), but is distinguished from Group II by the presence of large areas of open water colonized by free-floating and submersed aquatic herbs.

Group IV included four sites dominated by *Spiraea alba* var. *latifolia* and/or *Alnus incana*. Site age ranged from 15 to 35 years. These sites were characterized by high water table, generally high percent cover of *Sphagnum* spp., and intermediate tree and shrub cover. Cover of tussock-colonizing graminoids ranged from 0.5 to 5.5%. Depth of organic matter ranged from 46.5 to 189.1 cm (Table 2). This group corresponds to “shrub swamp” as defined by Reschke (1990), but is distinguished from Group I by the abundance of *Sphagnum* spp. in three of four sites.

Groups I, II, and III showed little variation in water chemistry (Table 3). Group IV was much lower in mean pH (field) than Groups I, II, and III, lower in mean alkalinity than groups I and III, and intermediate in mean conductivity between Group I and Groups II and III. Table 4 lists MIVs of three pH-sensitive taxa, *Sphagnum* spp., *Calamagrostis canadensis*, and *Carex stricta*, in the 11 sites sampled since 1992. While an association is suggested between *Sphagnum* spp. and more acidic sites, no clear pattern is observable between pH (lab) and importance values of *Calamagrostis canadensis* and *Carex stricta*.

Table 5. Means of five coefficients of similarity for four pairs of sites < 1 km apart compared to sites ≥ 1 km apart.

Distance between sites (km)	Number of site pairs	Jaccard	Ellenberg	Sørensen	Gleason	Spatz
< 1 km	4	0.43	0.65	0.59	0.79	0.14
≥ 1 km	101	0.31	0.44	0.47	0.60	0.08

Other relationships are also suggested by the TWINSpan ordination of sites (Tables 2 and 3). The three most recently abandoned sites (Ashfield 3, 4, and 5) showed compositional similarities as did two pairs of sites with a common water source, Williamsburg 1 and 2 (on Joe Wright Brook) and Ashfield 1 and 2 (on Stones Brook). Three pairs of geographically proximate sites were clustered together: Ashfield 1 and 2, Ashfield 4 and 5, and Conway 1 and 2. A comparison of means of five coefficients of similarity for pairs of sites < 1 km apart with those for sites ≥ 1 km apart (Table 5) suggests greater floristic similarity among closer sites.

Abiotic characteristics. Differences in mean depth to water table were much greater between sites (Table 2) than between transects within sites (Table 6). No substantial within-site differences were found in 6 of 10 sites. Where large within-site differences did occur, they were usually between the first transect (i.e., the transect closest to the dam) where water levels were highest, and subsequent transects where water levels were lower. The atypical pattern in Conway 3 resulted from the unusual topography of that site: three dams were present in 1995, but only the second dam was impounding water and only transect 3, which lay immediately upstream from the second dam, was affected.

Differences in mean depth of organic matter were also greater between sites (Table 2) than between transects within sites (Table 6). No substantial within-site differences were found in 3 of 11 sites. As with depth to water table, greatest within-site differences usually occurred between the first transect and subsequent transects. The small amount of organic matter immediately above the dam in most sites was probably due to repeated flushing as runoff moved rapidly through the gap in the abandoned dam. The five

sites with the greatest depth of organic sediments were all 16 years or older.

Water chemistry parameters followed a pattern similar to that for depth to water table and depth of organic matter, with larger differences between sites (Table 3) and much smaller differences within sites (Table 6).

Plant community types. One hundred fifty-one transects (including repeat samplings) and 219 species were clustered into five major community types in three hierarchical divisions using TWINSpan (Figure 1). The scatter plot of samples produced by detrended correspondence analysis using the software package CANOCO is shown in Figure 2 with numbers indicating the five community types identified by TWINSpan.

The five transects through standing water (labeled “1” in Figure 2) were removed and the analysis repeated (Figure 3). Comparison of the abiotic characteristics of each site suggests that Axis 1 corresponds to moisture gradient (transects to the right occurring in saturated soils and those to the left in increasingly drained soils) and Axis 2 corresponds to reflooding regime (lower transects are subject to more frequent, extensive, and longer-lasting reflooding than upper transects). Solid lines indicate that the plant communities identified by TWINSpan were ordinated by detrended correspondence analysis into contiguous groups with relatively few outliers.

Each of the five plant communities delineated by TWINSpan may be associated with a distinct physiographic zone within the study sites. Table 7 lists characteristic taxa for each zone (i.e., taxa with high MIVs in that zone and low MIVs in the other zones). Taxa with high MIVs in more than one zone are not included.

Zone 1, open water: *Najas flexilis*–*Utricularia vulgaris* Community

This zone was usually located immediately upstream from the beaver dam, although it sometimes occurred in depressions elsewhere in a site, as well. The zone was often largest in spring and after heavy rainfalls, especially in sites with an intact dam, but was usually reduced in size as summer progressed and in some sites dried up for a few weeks during prolonged drought. Organic sediments were thinnest and dissolved oxygen concentrations were lowest in this zone.

Table 6. Water chemistry characteristics by transect for the 15 study sites and depth to water table and depth of organic matter in unoccupied sites, summer, 1995. – Indicates data not available. *Indicates transects with one or more measurements of organic matter > 200 cm (see Materials and Methods). Numbers of depth measurements for each transect are shown in parentheses. See Table 2 for site abbreviations.

Site	Transect	pH (field)	Alkalinity (mg/l)	Conductivity (mhos)	Dis-solved Oxygen Concentration (mg/l)	Mean Depth of Water Table (cm)	Mean Depth of Organic Matter (cm)
Ashfd. 1	1	6.63	30.5	165	6.9	17.9 (7)	98.6 (7*)
	2	6.47	31.4	165	7.4	–	167.5 (8*)
	3	6.15	–	170	7.3	14.4 (7)	195.0 (7*)
Ashfd. 2	1	6.54	15.5	160	6.6	–	41.9 (8)
	2	6.55	24.0	160	7.3	2.1 (7)	180.0 (9*)
	3	6.55	–	155	7.5	2.0 (7)	188.6 (7*)
Ashfd. 3	1	5.63	1.5	36	10.8	7.0 (9)	31.4 (11)
	2	5.67	1.0	35	12.7	14.6 (9)	79.2 (13)
	3	5.99	–	36	14.6	22.1 (9)	76.4 (11)
	4	–	–	–	–	13.1 (8)	76.3 (8)
Ashfd. 4	1	6.72	17.0	90	5.8	–	42.5 (8)
	2	6.70	50.5	170	3.6	–	47.9 (7)
	3	–	–	110	–	–	66.7 (9)
	4	6.02	–	110	6.8	6.4 (7)	130.9
	5	6.14	–	110	6.1	4.7 (7)	138.8 (8*)
Ashfd. 5	1	6.55	19.0	140	3.4	–	60.0 (3)
	2	5.97	22.5	160	1.0	–	35.0 (3)
	3	–	21.4	–	–	–	52.5 (2)
	4	–	–	–	–	–	68.3 (3)
Ashfd. 6	1	5.89	18.0	110	4.5	–	–
	2	5.77	48.0	110	5.3	–	–
	3	6.06	18.5	110	5.0	–	–
	4	6.33	–	90	2.8	–	–
	5	–	–	110	3.2	–	–
	6	6.88	–	120	1.8	–	–
Conway 1	1	6.47	14.5	140	–	5.3 (4)	38.8 (4)
	2	6.44	–	150	–	0.8 (4)	53.8 (4)
	3	6.35	–	145	–	2.3 (4)	114.1 (7)
	4	6.28	–	140	–	1.5 (4)	98.6 (7)
Conway 2	1	5.21	1.5	35	–	0.3 (4)	200.0 (4*)
	2	5.46	4.0	35	–	0.7 (7)	160.0 (3*)
	3	5.20	–	50	–	2.3 (7)	200.0 (2*)
	4	5.19	–	45	–	2.3 (4)	200.0 (2*)
	5	–	–	60	–	3.3 (4)	–
	6	–	–	50	–	–	–

Table 6. Continued.

Site	Tran- sect	pH (field)	Alka- linity (mg/l)	Con- duc- tivity (mhos)	Dis- solved	Mean Depth of Water Table (cm)	Mean Depth of Organic Matter (cm)
					Oxygen Concen- tration (mg/l)		
Conway 3	1	6.24	14.0	80	—	14.4 (5)	51.1 (9)
	2	6.48	29.0	85	—	2.2 (5)	55.0 (6)
	3	6.43	—	80	—	9.8 (5)	70.8 (6)
	4	6.43	—	80	—	—	82.5 (2)
	5	—	—	—	—	—	108.3 (3)
Conway 4	1	5.15	16.5	55	—	1.3 (4)	43.3 (6)
	2	5.18	19.0	55	—	7.0 (4)	45.0 (5)
	3	5.32	—	60	—	6.8 (4)	53.8 (4)
	4	—	—	55	—	9.3 (4)	45.0 (2)
	5	—	—	60	—	—	—
Conway 5	1	6.15	19.5	120	2.1	—	—
	2	—	39.0	105	2.0	—	—
	3	6.37	—	110	1.4	—	—
	4	—	—	115	1.8	—	—
	5	6.61	—	75	2.6	—	—
	7	6.68	—	145	1.0	—	—
Goshen 1	1	6.51	18.5	160	2.0	—	—
	2	—	21.0	165	2.4	—	—
	3	7.12	—	165	4.8	—	—
	4	—	—	180	2.6	—	—
	5	—	—	170	4.2	—	—
Willb. 1	1	6.17	10.5	70	6.9	6.3 (6)	115.7 (7*)
	2	6.11	15.5	60	7.3	18.1 (7)	107.9 (7)
	3	6.21	—	60	3.7	16.0 (7)	113.3 (6)
	4	—	—	65	3.7	—	115.8 (6)
Willb. 2	1	6.33	25.5	60	9.3	32.8 (4)	100.0 (6*)
	2	6.44	29.0	60	10.2	26.0 (4)	85.0 (5)
	3	6.51	—	60	8.9	34.0 (3)	141.7 (3)
	4	6.15	—	60	9.4	40.0 (1)	146.3 (4)
Worth. 1	1	4.79	0.5	50	—	—	—
	2	4.90	3.5	35	—	—	—

Of the 43 species sampled in Zone 1, floating, submersed, and emergent hydrophytes were the most common life forms. Mats of *Lemna minor*, *Najas flexilis*, and *Utricularia vulgaris* often predominated in deeper water, while stands of *Sparganium an-*

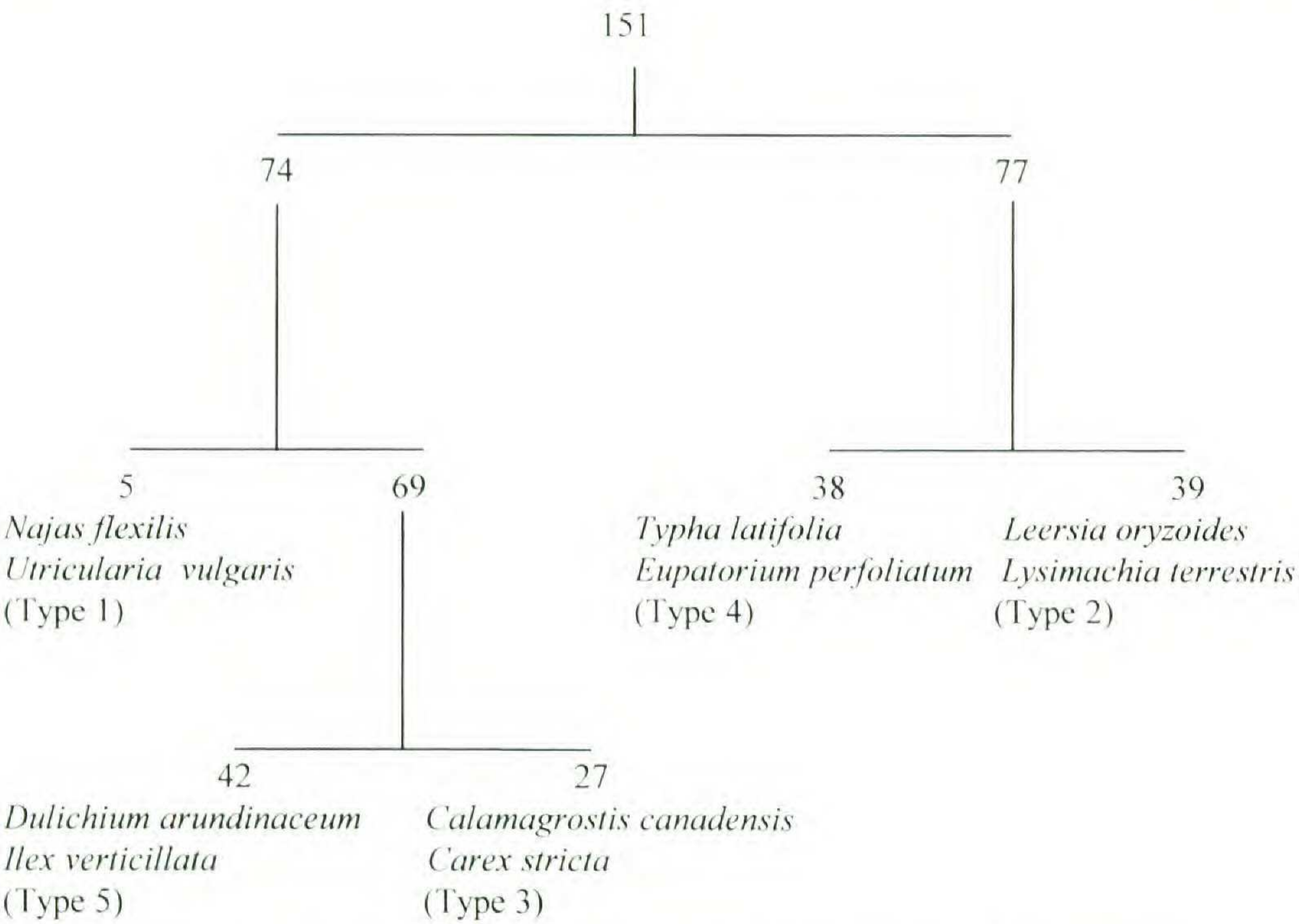


Figure 1. Five major vegetation types in 151 transects as delineated with TWINSpan. Numbers indicate number of transects in each division.

drocladum (Engelm.) Morong occurred in shallower water. Rooted hydrophytes such as *Brasenia schreberi* J. F. Gmel., *Nuphar variegata* Durand, *Polygonum amphibium* L., and *Potamogeton* spp. also occurred, though less frequently, in this zone. Where open water occurred due to reoccupation of a site that had been abandoned for a number of years, some of the pre-existing vegetation persisted, including woody taxa such as *Acer rubrum* and *Spiraea alba* var. *latifolia*, and tussock-colonizing graminoids.

Zone 2, mud flat: *Leersia oryzoides*–*Lysimachia terrestris* Community

This zone of recently exposed pond bottom sediments occurred immediately upstream from the beaver dam and the open water of Zone 1. It usually attained its maximum extent in late summer and was frequently reflooded during the growing season. The stream often cut a narrow channel through the bottom sediments of this zone, increasing flow and resulting in higher mean dissolved oxygen concentration than in the other zones.

Of the 146 species sampled in Zone 2, emergent hydrophyte was the most common life form. *Leersia oryzoides* was the most

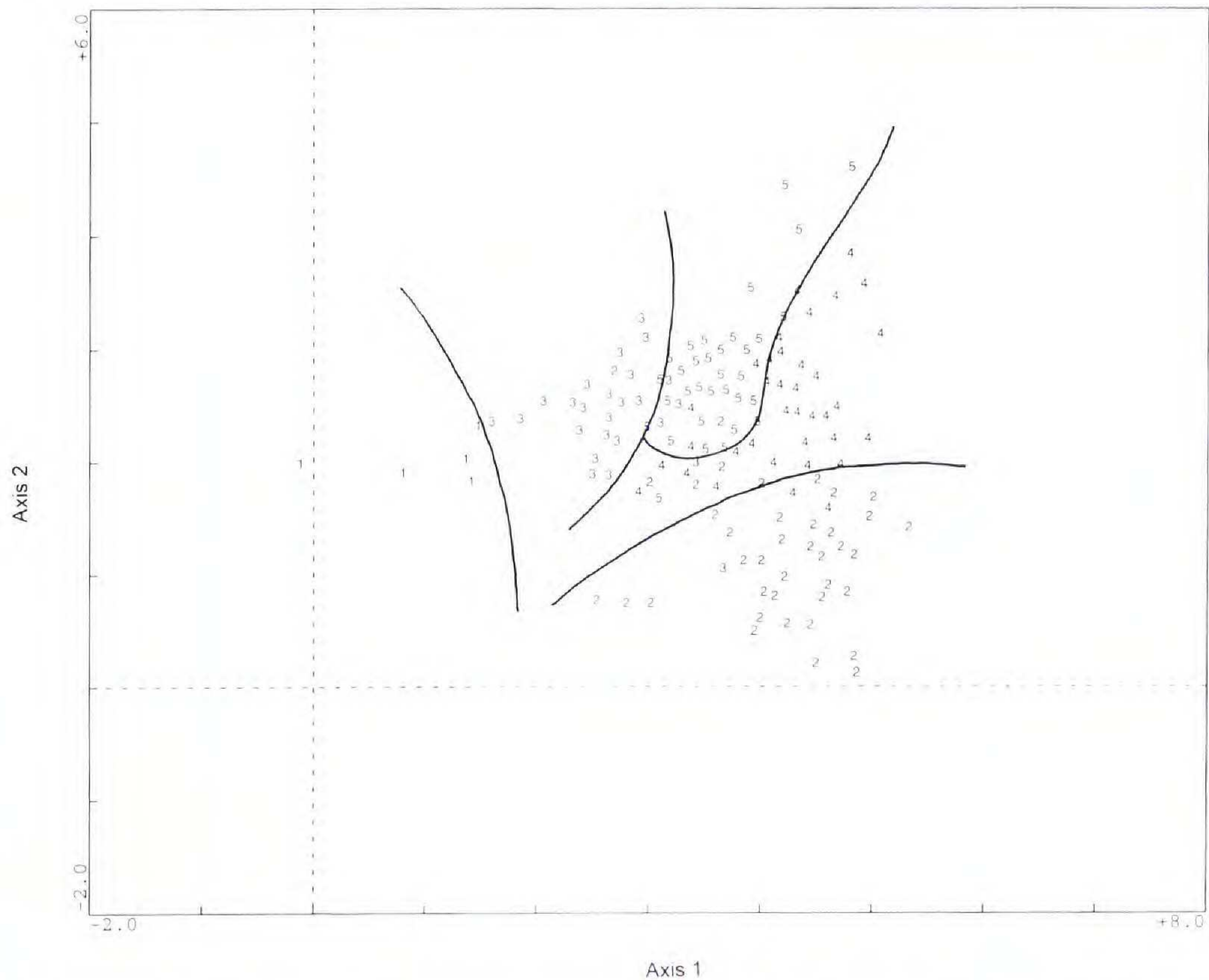


Figure 2. Plot of detrended correspondence analysis sample ordination, Axes 1 and 2, for transects in 15 beaver-impacted wetlands based on modified importance values ≥ 5 . Numbers indicate five community types as identified by TWINSpan: 1 – *Najas flexilis*–*Utricularia vulgaris* Community, 2 – *Leersia oryzoides*–*Lysimachia terrestris* Community, 3 – *Calamagrostis canadensis*–*Carex stricta* Community, 4 – *Typha latifolia*–*Eupatorium perfoliatum* Community, 5 – *Dulichium arundinaceum*–*Ilex verticillata* Community.

important species of this zone in most sites, although *Lysimachia terrestris* was even more important than *L. oryzoides* in a few sites. Other important species included *Agrostis gigantea*, *Eleocharis acicularis*, and *Galium tinctorium*. Taxa sometimes occurring in Zone 2 that may have persisted from before the last re-occupation included *Carex stricta*, *Calamagrostis canadensis*, *Scirpus cyperinus*, *Spiraea alba* var. *latifolia*, and *S. tomentosa*.

Zone 3, wet meadow: *Calamagrostis canadensis*–*Carex stricta* Community

Zone 3 was located farther upstream on soils that were subject to regular fluctuations of the water table. Among the five zones, mean depth of organic sediments was greatest in this zone.

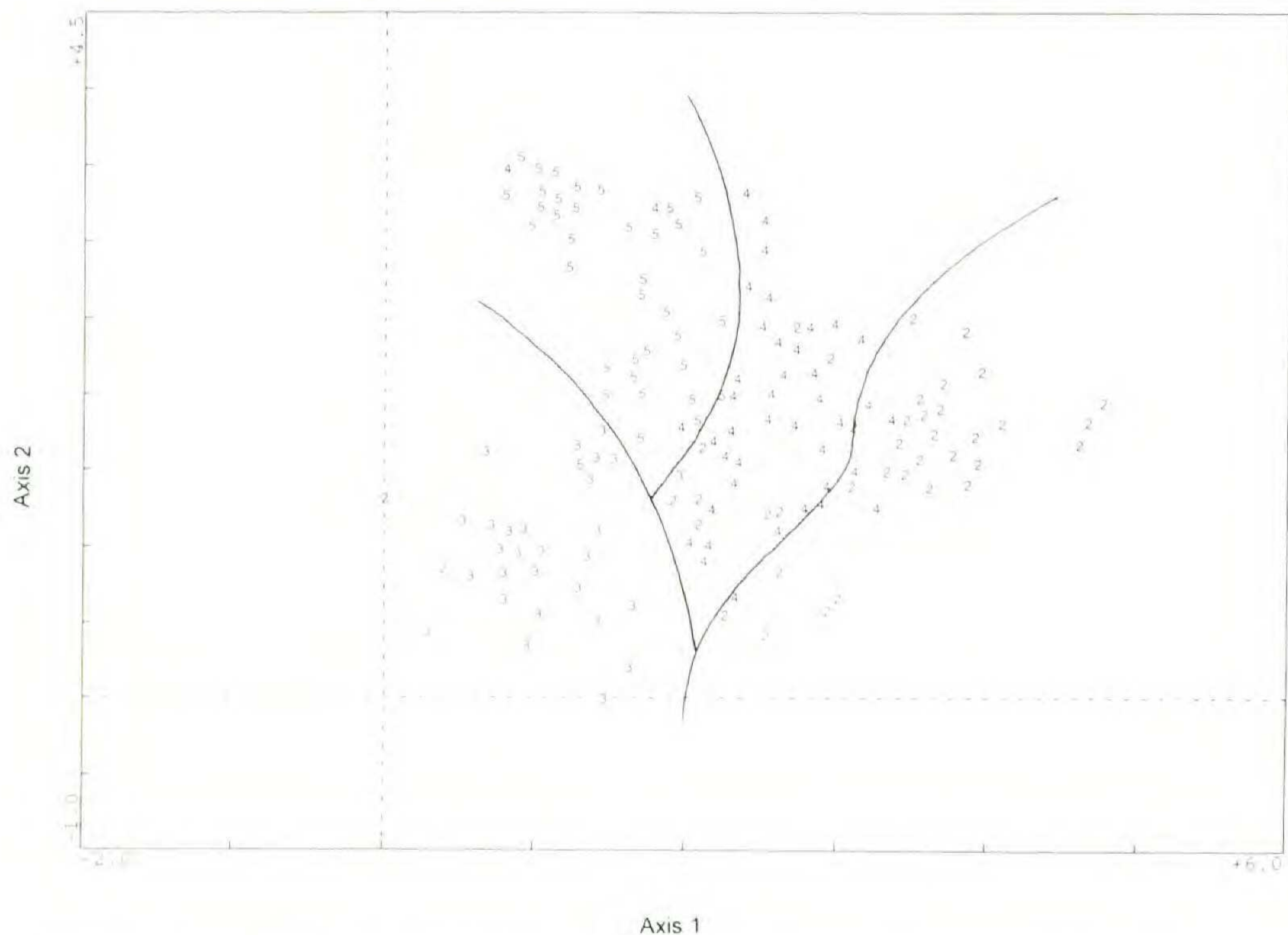


Figure 3. Plot of detrended correspondence analysis sample ordination, Axes 1 and 2, for transects in 15 beaver-impacted wetlands based on modified importance values ≥ 5 after removing Zone 1 transects. Solid lines indicate that the four community types identified by TWINSpan are ordinated by CANOCO into contiguous groups with relatively few outliers. Axis 1 represents a moisture gradient, with wettest transects on the left, driest transects on the right. Numbers indicate four community types identified by TWINSpan: 2 – *Leersia oryzoides*–*Lysimachia terrestris* Community, 3 – *Calamagrostis canadensis*–*Carex stricta* Community, 4 – *Typha latifolia*–*Eupatorium perfoliatum* Community, 5 – *Dulichium arundinaceum*–*Ilex verticillata* Community.

Of the 147 species sampled in Zone 3, emergent hydrophyte was the most common life form. Tussock-forming or tussock-colonizing graminoids predominated in many wet meadows, sometimes forming nearly pure stands. A tussock forms when dead culms and leaves persist at the plant base. With each new season the plant grows higher, sometimes forming a pillar 0.5 m or more above the wet substrate. Three graminoids associated with tussocks in this study included *Carex stricta*, *Calamagrostis canadensis*, and *Phalaris arundinacea*. It is likely that *C. stricta* was responsible for formation of most tussocks which were later colonized by *C. canadensis* and *P. arundinacea*, sometimes to the exclusion of *C. stricta*. Other taxa that frequently invaded

Table 7. Characteristic taxa for the five physiographic zones as identified by TWINSpan. Included are taxa with high MIVs in each zone and low MIVs in the other zones. Taxa with high MIVs in more than one zone are not included.

Taxa for Zones 1, 2, and 3	Taxa for Zones 4 and 5
ZONE 1 <i>Lemna minor</i> L. <i>Najas flexilis</i> (Willd.) Rostk. & Schmidt <i>Potamogeton natans</i> L. <i>Utricularia vulgaris</i> L.	ZONE 4 <i>Aster puniceus</i> L. <i>Carex atlantica</i> L. Bailey <i>Carex comosa</i> F. Boott <i>Carex crinita</i> Lam. <i>Carex stipata</i> Muhl. <i>Eupatorium maculatum</i> L. <i>Eupatorium perfoliatum</i> L. <i>Glyceria canadensis</i> (Michx.) Trin. <i>Impatiens capensis</i> Meerb. <i>Juncus effusus</i> L. <i>Polygonum sagittatum</i> L. <i>Spiraea tomentosa</i> L. <i>Triadenum virginicum</i> (L.) Raf. <i>Typha latifolia</i> L.
ZONE 2 <i>Agrostis gigantea</i> Roth <i>Eleocharis acicularis</i> (L.) Roem. & Schult. <i>Eleocharis ovata</i> (Roth) Roem. & Schult. <i>Eleocharis palustris</i> L. <i>Euthamia graminifolia</i> (L.) Nutt. <i>Galium tinctorium</i> L. <i>Galium trifidum</i> L. <i>Leersia oryzoides</i> (L.) Sw. <i>Ludwigia palustris</i> (L.) Elliott <i>Lycopus virginicus</i> L. <i>Lysimachia terrestris</i> (L.) BSP. <i>Mentha arvensis</i> L. <i>Penthorum sedoides</i> L. <i>Scirpus atrovirens</i> Willd. <i>Scirpus cyperinus</i> (L.) Kunth <i>Solidago canadensis</i> L.	ZONE 5 <i>Acer rubrum</i> L. <i>Alnus incana</i> (L.) Moench <i>Betula alleghaniensis</i> Britton <i>Betula papyrifera</i> Marshall <i>Bidens cernua</i> L. <i>Carex vulpinoidea</i> Michx. <i>Cornus amomum</i> Mill. <i>Drosera rotundifolia</i> L. <i>Dulichium arundinaceum</i> (L.) Britton <i>Equisetum arvense</i> L. <i>Ilex verticillata</i> (L.) A. Gray <i>Myrica gale</i> L. <i>Onoclea sensibilis</i> L. <i>Osmunda regalis</i> L. <i>Prunus serotina</i> Ehrh. <i>Salix sericea</i> Marshall <i>Solidago patula</i> Muhl. <i>Sphagnum</i> spp. <i>Spiraea alba</i> DuRoi var. <i>latifolia</i> (Aiton) Dippel <i>Thelypteris palustris</i> Schott <i>Vaccinium corymbosum</i> L.
ZONE 3 <i>Calamagrostis canadensis</i> (Michx.) P. Beauv. <i>Carex intumescens</i> Rudge <i>Carex lacustris</i> Willd. <i>Carex stricta</i> Lam. <i>Hypericum ellipticum</i> Hook. <i>Phalaris arundinacea</i> L. <i>Viburnum dentatum</i> L. var. <i>lucidum</i> Aiton	

tussock crowns and/or colonized hollows included *Carex intumescens*, *Galium tinctorium*, *Impatiens capensis*, *Lysimachia terrestris*, and *Triadenum virginicum*. Taxa sometimes occurring in Zone 3 that may have persisted through previous occupations included *Acer rubrum*, *Alnus incana*, *Ilex verticillata*, *Salix sericea*, *Spiraea alba* var. *latifolia*, and *S. tomentosa*.

Zone 4, drier meadow: *Typha latifolia*–*Eupatorium perfoliatum* Community

Zone 4 occurred still farther upstream on moist soils seldom affected by water level fluctuations.

Of the 155 species recorded in Zone 4, the major life forms were emergent hydrophyte, shrub, and tree seedling. The most important species was *Typha latifolia*, which often occurred in large pure stands anchored to the wetland substrate by proliferating creeping rhizomes. Common graminoids included *Carex crinita*, *Glyceria canadensis*, *Juncus effusus*, and *Leersia oryzoides*. Other herbs present were *Eupatorium maculatum*, *E. perfoliatum*, *Euthamia graminifolia*, *Impatiens capensis*, *Onoclea sensibilis*, *Polygonum sagittatum*, *Solidago canadensis*, *Thelypteris palustris*, and *Triadenum virginicum*. *Alnus incana* and *Spiraea alba* var. *latifolia* were the most important shrubs.

Zone 5, dry meadow/upland margin: *Dulichium arundinaceum*–*Ilex verticillata* Community

Zone 5 occurred farther upstream, usually on drier, seldom re-flooded soils in a narrow band along the wetland/upland ecotone. In most sites this zone was sampled only by one or two quadrats at the ends of transects through Zones 3 and 4. In only three sites were transects placed exclusively through Zone 5: Conway 1, Conway 2, and Conway 4. Because of their location close to the watershed boundary and with little topographic gradient, these three sites exhibited an unusual combination of high water table and large percent cover of shrubs and trees.

Of the 128 species found in Zone 5, emergent hydrophyte, shrub, and tree sapling were the most common life forms. *Dulichium arundinaceum* was the most important taxon in this zone (mostly due to its high MIV in Conway 2) followed by *Spiraea alba* var. *latifolia*, *Ilex verticillata*, and *Alnus incana*. Woody taxa more typical of the surrounding upland including *Acer rubrum*,

Betula alleghaniensis, *B. papyrifera*, *B. populifolia* Marshall, and *Prunus serotina* Ehrh. could also be found in this zone, though in low densities. A diverse herbaceous stratum grew under this canopy including *Carex comosa*, *C. atlantica*, *C. stricta*, *Galium tinctorium*, *Onoclea sensibilis*, *Osmunda regalis*, and *Scirpus cyperinus*. Species of *Sphagnum* were abundant, often forming a nearly continuous mat on the substrate beneath the herb and shrub canopy.

All the study sites included three or more zones; four sites included all five zones. In some sites, zones were arranged in sequence along the hydrological gradient. Frequently, zone arrangement was more complex, with a lateral progression of zones parallel to the stream channel or with isolated patches of Zones 4 and 5 occurring within Zones 1, 2, and 3, especially where shrubs, typically *Viburnum* spp., *Salix* spp., or *Spiraea* spp., had survived inundation. Detailed maps of the vegetation zones of each site are presented in McMaster (1997).

Figure 4 is a bi-plot of the results of canonical correspondence analysis showing the direction and strength of the environmental variables. Numbers correspond to the five major plant communities identified by TWINSpan. Transects separated out most clearly along the gradients of site age, depth of organic matter, pH (field), and alkalinity, suggesting that these factors were most closely related to the distribution of plant communities. Mean distance to water table, pH (lab), conductivity, and dissolved oxygen concentration gradients did not appear to relate closely to plant community distributions.

Succession. Arrows in Figure 5 indicate the successional development of vegetation in a transect over time; the tail of each arrow indicates the location of the initial sampling, the head of the arrow the position of the final sampling. Arrow length is a measure of change in species composition of a site between two samplings. As no site was occupied when first sampled, all developmental sequences originate in Zones 2 or 3.

Three successional pathways are suggested by Figure 5 and depicted schematically in Figure 6. In the first pathway (Figure 5, solid arrows), the *Najas flexilis*–*Utricularia vulgaris* Community invades sites that have been flooded for at least one year. After abandonment, the sites begin to drain and the *Leersia ory-*

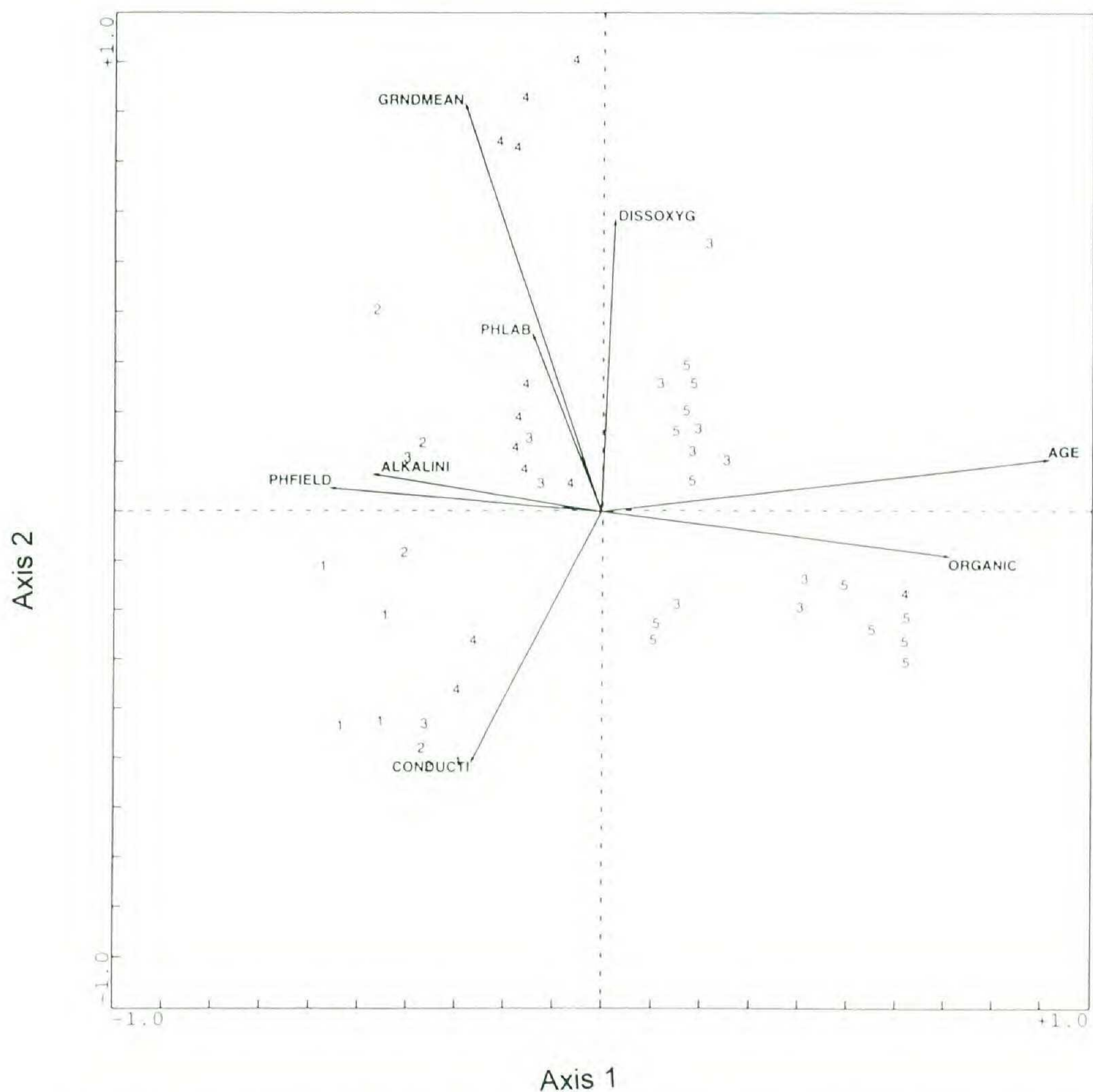


Figure 4. Bi-plot of canonical correspondence analysis sample ordination, Axes 1 and 2, for 48 transects with eight environmental variables. Arrows indicate the direction and strength of each environmental variable. GRNDMEAN = Depth of water table; DISSOXYG = Dissolved oxygen concentration; PHFIELD = pH (field); PHLAB = pH (lab); ALKALINI = Alkalinity; ORGANIC = Depth of organic matter; CONDUCTI = Conductivity; AGE = Site age. Numbers indicate five community types as identified by TWINSPAN: 1 – *Najas flexilis*–*Utricularia vulgaris* Community, 2 – *Leersia oryzoides*–*Lysimachia terrestris* Community, 3 – *Calamagrostis canadensis*–*Carex stricta* Community, 4 – *Typha latifolia*–*Eupatorium perfoliatum* Community, 5 – *Dulichium arundinaceum*–*Ilex verticillata* Community.

zoides–*Lysimachia terrestris* Community invades newly-exposed pond bottom. As draining continues, the *L. oryzoides*–*L. terrestris* Community is rapidly replaced by the *Typha latifolia*–*Eupatorium perfoliatum* Community. Within 10 to 15 years the *Dulichium arundinaceum*–*Ilex verticillata* Community is evident. In some sites, large pure stands of *T. latifolia* achieve dominance. Suc-

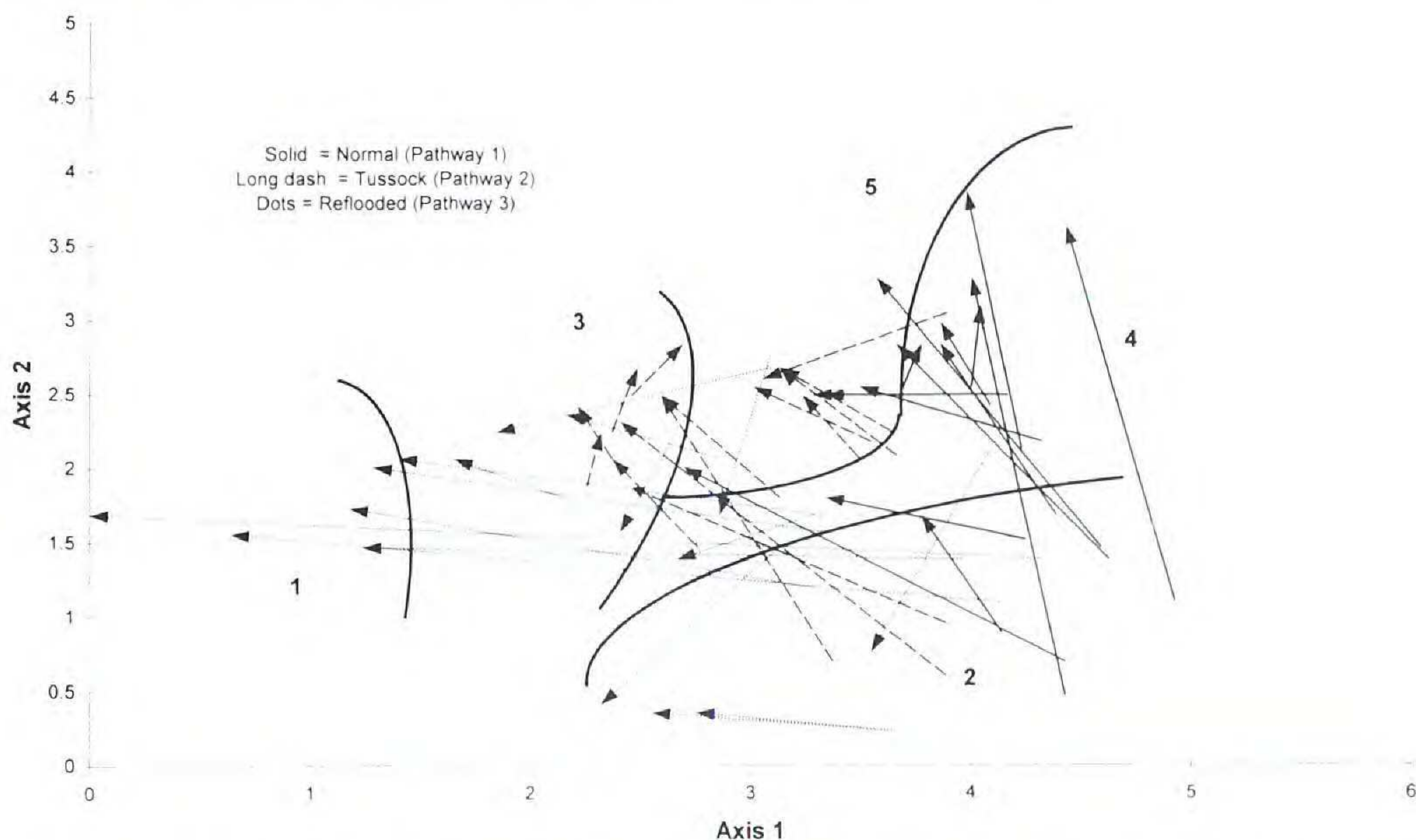


Figure 5. Plot of detrended correspondence analysis sample ordination, Axes 1 and 2, for transects in 15 beaver-impacted wetlands based on modified importance values ≥ 5 . Lines connect positions of transects sampled over 10 and 15-year intervals. Arrowheads indicate the most recent sampling. Axis 1 represents a moisture gradient, with wettest transects on the left, driest transects on the right. Numbers refer to five community types identified by TWINSpan: 1 – *Najas flexilis*–*Utricularia vulgaris* Community, 2 – *Leersia oryzoides*–*Lysimachia terrestris* Community, 3 – *Calamagrostis canadensis*–*Carex stricta* Community, 4 – *Typha latifolia*–*Eupatorium perfoliatum* Community, 5 – *Dulichium arundinaceum*–*Ilex verticillata* Community.

cession at this point often appears to be slowed or halted. Should a site remain undisturbed for more than 15 years and the soils continue to drain, succession along Pathway 1 may continue, eventually leading to development of forested wetland or upland forest. This pathway was observed in three sites: Conway 3, Conway 4, and Williamsburg 2.

A second pathway (Figure 5, dashed arrows) begins as in Pathway 1 with the *Najas flexilis*–*Utricularia vulgaris* Community succeeded by the *Leersia oryzoides*–*Lysimachia terrestris* Community. However, as the sites drain following this course of development, the *L. oryzoides*–*L. terrestris* Community is replaced within five to ten years by the *Calamagrostis canadensis*–*Carex stricta* Community. Succession may be slowed or may cease for 10–15 years or more in some sites. Sites in which this pathway was observed include Ashfield 1, Ashfield 2, Williamsburg 1, and a portion of Conway 3. The four shortest dashed arrows represent

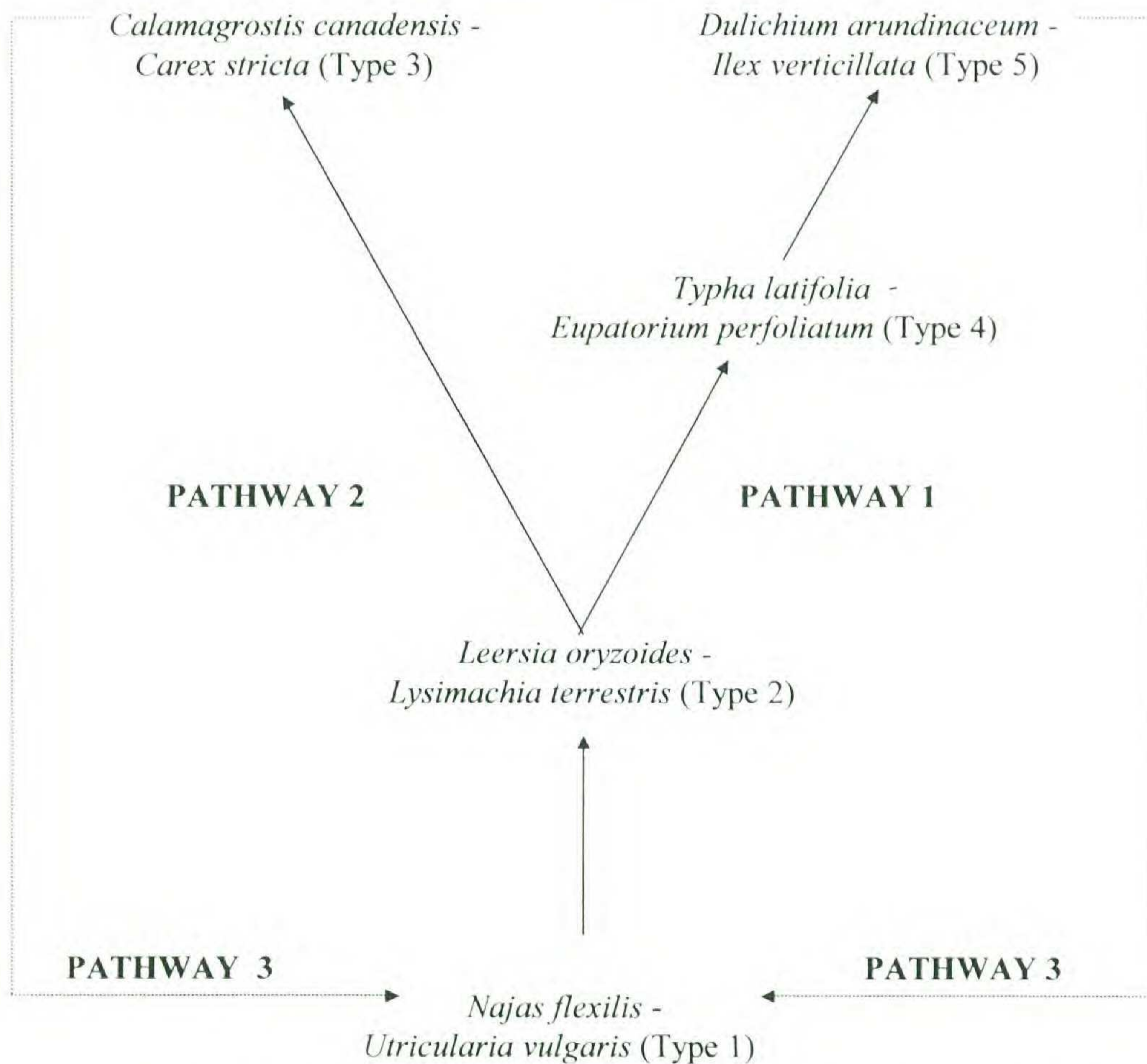


Figure 6. Schematic representation of successional pathways observed in beaver-impacted wetlands.

transects in Conway 2 where the rate of succession was slow and where small, simultaneous increases in MIV of species associated with the *C. canadensis*-*C. stricta* Community and the *Dulichium arundinaceum*-*Ilex verticillata* Community were observed.

When sites dominated by the *Leersia oryzoides*-*Lysimachia terrestris* Community or the *Calamagrostis canadensis*-*Carex stricta* Community are inundated following reoccupation, they follow a third, retrogressive pathway (Figure 5, dotted arrows), with reinvasion by the *Najas flexilis*-*Utricularia vulgaris* Community if standing water covers much of the site, or by the *L. oryzoides*-*L. terrestris* Community if exposed mud flats predominate. Tussock-colonizing species and some water-tolerant shrubs survive from the earlier communities. This pathway was observed in four sites: Ashfield 3, Ashfield 4, Ashfield 5, and in a portion of Conway 3.

Acer rubrum, while present in all 15 study sites, did not occur in large quantities upon initial sampling in any site (Mean Percent Cover = 1.3 ± 0.2 for all sampled transects; range 0.1 to 8.1%). In only one site, Williamsburg 1, was there a sizable increase in percent cover of *A. rubrum* between samplings (0.7% in 1984 to 12.2% in 1994). In four sites there was a small increase ($< 3.0\%$), while in six other sites a substantial decline was observed (McMaster 1989; McMaster 1997).

DISCUSSION

While the TWINSPLAN classification suggests the importance of water table depth in the study sites, canonical correspondence analysis reveals only a weak correlation between depth to water table and plant community composition. Our observations of the study sites over 15 years suggest that composition and structure of vegetation in beaver-impacted wetlands are strongly influenced not simply by water table depth but by a complex of hydrological factors including frequency, extent, and duration of reflooding. Reflooding regime appears to be a function of at least three major factors in beaver-impacted wetlands: topographic gradient, size of the watershed upstream from a site, and condition of the abandoned beaver dam.

Sites with low topographic gradient, a large watershed, and/or an intact beaver dam normally drain slowly after abandonment and reflood frequently during spring runoff and following major precipitation events. These sites generally revegetate slowly and favor species tolerant of hydric soils. Because conditions are relatively uniform throughout, zonation is not pronounced in these sites. Tussock-forming and tussock-colonizing species appear to enjoy an advantage in frequently reflooded sites because the microhabitat is elevated above high water level.

Sites with high topographic gradient and a small watershed but lacking an intact beaver dam normally drain more rapidly and are less likely to be subject to seasonal reflooding. These sites generally revegetate quickly and are readily invaded by species typical of drier upland habitat. Zonation is often better developed in these sites and tussock-colonizing species are less common than in sites that are frequently reflooded. High gradient sites are often created when beaver colonies are removed, dams excavated,

and streams channelized in response to the threat of flooding to roads, railroad tracks, or agricultural fields.

Tussock-forming graminoids create a highly irregular surface with tussock crowns often 0.5 m or more above the intervening hollows. In such a complex microtopography, a single measurement of depth to water table may bear little relationship to the hydrological conditions experienced by all members of the plant community. In a study of six peatlands in Alberta, Canada, Karlin and Bliss (1984) observed pronounced differences, not only in soil moisture but also in substrate chemistry, that were found to influence differences in plant community composition between tussock crowns and hollows.

Species composition of recently abandoned beaver wetlands in this study is clearly related to depth to water table. As sites age, however, the relationship between water table and composition becomes less clear. Succession in some draining beaver ponds appears to follow the classical hydrarch successional sequence from submersed or floating-leaved hydrophytes to emergents to small shrubs and trees (Pathway 1). The invasion of tussock-colonizing species (Pathway 2), however, appears to alter the course of succession in some sites. While the tussock and hollow microtopography might be expected to provide niches for a greater diversity of species and opportunities for more rapid successional development, in our study sites diversity declined and succession appeared to slow or stop following tussock formation, probably a result of intense root competition within tussocks and the influence of anoxic soils and deep shade in hollows.

The appearance of some woody species along the upland margins of old, well-drained sites was likely a result of recruitment from the surrounding upland forest. However, the occurrence of certain shrubs, especially species of *Spiraea*, *Alnus*, and *Viburnum*, immediately above the dam in sites of all ages suggests that many had survived inundation and continued to grow in the abandoned site. Similarly, tussock-colonizing graminoids appeared to be well-suited to fluctuating water tables and able to survive repeated occupations and abandonments. Some aspects of the composition of a site may thus be more or less indifferent to the current conditions, and may exist because of conditions that persisted or events that occurred years or even decades in the past.

Forested wetlands, especially those dominated by *Acer rubrum*, are a common feature of the landscape in the glaciated north-

eastern United States, covering 8 to 16% of some counties in eastern Massachusetts. West of the Connecticut River in Massachusetts, on the other hand, forested wetlands are uncommon, covering less than 3% of the land surface, probably due to greater topographic relief and the distinctive surficial geology and runoff patterns of that region (Golet et al. 1993). Could long-abandoned beaver wetlands in the study area follow a developmental pathway to forested wetland rather than to upland forest as described above? In only one of our sites, Williamsburg 1, was a major trend toward forested wetland observed over the duration of this study. Soil moisture and nutrient availability, both of which result from topographic gradient, may be predictors of long-term changes in the woody composition of the study sites. Where topographic gradient is greatest, even an intact abandoned beaver dam may not affect the water table enough to keep upland species from invading. Where topographic gradient is low, the water table may remain sufficiently high and nutrients in limited supply, even in the absence of beavers or their dams, so as to prevent the growth of *Acer rubrum* beyond the seedling stage (Golet et al. 1993; Moizuk and Livingston 1966). Sedge tussocks, by providing a raised substrate, have been observed to facilitate establishment and growth of *Acer rubrum* seedlings (Golet et al. 1993), a phenomenon observed in Williamsburg 1, but in other sites in this study tussocks more often excluded woody species rather than promoted them. The two sites with greatest percent cover of *A. rubrum* in 1995 were also among the most acidic, suggesting that low pH, which tends to inhibit nutrient uptake, may play a role in regulating growth of trees in long-abandoned sites.

Wetland seed banks usually include species of local provenance (Smith and Kadlec 1983; ter Heerdt and Drost 1994; van der Valk and Davis 1978). In this study several woody species present in the adjacent upland were represented in the wetland, notably *Acer rubrum*, *Betula populifolia*, *Picea abies*, and *Pinus strobus*, although few individual seedlings or saplings fell within sampled quadrats. Upland species occurred in three sites that have followed Pathway 1 for 20 years or more. Further study will be required to determine whether and to what degree the adjacent upland vegetation influences later successional stages in the study sites.

Among the water chemistry parameters examined in this study, pH (field) and alkalinity proved to be most strongly associated

with plant composition. In the four oldest, most acidic sites (Group IV), pH (field) and alkalinity decline, possibly as a result of the presence of organic acids within the accumulating sediments, which may be a result of the metabolic activity of *Sphagnum* spp. itself. In younger sites water chemistry appears to be less important than reflooding regime in influencing composition and structure of vegetation.

The beaver-impacted wetlands in this study were spatially and temporally complex. Site physiography was influenced by geological factors such as basin morphology, outcrops of bedrock, and glacial erratics; by beaver artifacts such as dams, lodges, and food caches; and by human artifacts such as walls, road fills, and excavations. All these factors affect moisture gradient, which in turn influences vegetational composition and structure. Furthermore, some members of the wetland plant community, including several shrubs and tussock-colonizing graminoids, play a significant role in altering site physiography as they create their own elevated soils and thus are buffered against fluctuating water levels. Finally, the repeated occupation and abandonment of sites by beavers, their foraging and dam-building, and periodic human disturbances such as trapping, filling, and draining, make these wetlands dynamic, ever-changing systems.

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